Feeding behavior and bioenergetic balance of the great scallop (*Pecten maximus*) and the blue mussel (*Mytilus edulis*) in a low seston environment and relevance to suspended shellfish aquaculture.

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Scientific environment

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In memory of Else O. Hummervoll

CONTENTS

ABSTRACT

The length of the rugged Norwegian coastal line including all islands exceeds the circumference of the earth, and the coastal zone contains many sheltered areas that are potentially suitable for bivalve farming. However, a large fraction of the coastal environment exhibits close to oligotrophic conditions and has significantly lower seston (e.g. food) concentration compared to most bivalve aquaculture sites currently operating worldwide. Aquaculture in low seston environments is a concern, partly because of the food requirement for bivalves to grow (e.g. particulate organic carbon (POC) ~ 200 µg L^{-1} or chlorophyll *a* (Chl *a*) ~ 1 mg L^{-1}), but also because bivalves were reported to stop feeding at low seston concentrations (Chl *a* between 0.5 to 0.9 µg L^{-1}). Low seston environments have an increased risk of food depletion that can reduce bivalve production due to food limitation, especially when bivalves are kept at high stocking density as in culture. In order to manage bivalve farming in low seston environments there is a need for bivalve production and carrying capacity models. The objective of the thesis was to study the functional feeding responses of two commercially important bivalve species (*Pecten maximus* and *Mytilus edulis*) to the dietary conditions in a natural low seston environment. Further objectives were to determine the net zero growth and net zero energy balance of the bivalves to help facilitate growth predictions. On a cultivation unit scale, the aim was to describe physical and biological components of seston depletion processes in long-line suspension culture, to optimize cultivation unit design, carrying capacity assessment and site selection.

Studies were carried out to facilitate an improved understanding of the seasonal feeding behavior, physiology and growth of the great scallop (*P. maximus*) and the blue mussel (*M. edulis*) under natural low (e.g. suspended particulate matter (SPM) < 1 mg L^{-1} or Chl *a* < 1.5 mg L^{-1}) and diluted seston concentrations and to provide data for aquaculture and ecosystem models. The results were novel in that they showed that these species do not stop feeding, but rather maintain intermediate to high feeding rates at all low seston concentrations employed. The feeding response to seston quantity was unimodal as previously reported for scallops and mussels, but the response curve was skewed toward lower seston concentrations. Positive tissue growth was detected at seston concentrations of 80 µg POC L^{-1} and 0.4 µg Chl *a* L^{-1}, which is less than half the values previously reported.

The ability of the bivalves to grow under the low seston quantities was primarily caused by continuous feeding at typically high rates and the high net absorption efficiency (range 40 – 80%). Net energy balance predictions for both species overestimated actual growth owing to a wide range of factors including; the inability of bulk seston characteristics to adequately characterize the seasonably variable energy content of the seston and spawning. To increase the accuracy of growth estimates, the biopolymeric constitute of seston should be considered as an alternative to utilizing constant POC/energy conversion factors for ingested food.

The spatial distribution of mussel condition index in a long-line (200 x 15 meter) mussel cultivation unit was studied in relation to physical flow reduction and seston depletion by mussel grazing. The food availability, expressed as the product of current speed and Chl *a* concentration, decreased to less than 20% of ambient within the first 30 meters of the unit. The strong reduction in food availability was the apparent cause of the lengthwise reduction in condition index detected from the edges toward the centre of the unit. The physical and biological data obtained from the long-line mussel unit was used to develop a model of current speed reduction and production capacity according to cultivation unit layout. The model output highlighted the need to optimize the farm length to width ratio to reduce seston depletion and improve flow characteristics. The model has increased the awareness of measuring current speed and seston concentration to identify suitable farming sites in Norway and has motivated farmers to rearrange the farm layout.

LIST OF PAPERS:

This thesis is based on the following publications and manuscript, which are referred to in the text by their Roman numerals.

I. Strohmeier T, Strand Ø, Cranford P (2009) Clearance rates of the great scallop (*Pecten maximus)* and blue mussel (*Mytilus edulis)* at low natural seston concentrations. Marine Biology 156: 1781-1795

II. Strohmeier T, Strand Ø, Cranford P, Krogness C (Manuscript) Scallop (*Pecten maximus*) and mussel (*Mytilus edulis*) tissue growth, net energy balance and physiological response to natural low seston concentrations.

III. Strohmeier T, Aure J, Duinker A, Castberg T, Svardal A, Strand Ø (2005) Flow reduction, seston depletion, meat content and distribution of diarrhetic shellfish toxins in a long-line blue mussel (*Mytilus edulis*) farm. Journal of Shellfish Research 24: 15-23

IV. Aure J, Strohmeier T, Strand Ø (2007) Modelling current speed and carrying capacity in long-line blue mussel (*Mytilus edulis*) farms. Aquaculture Research 38: 304-312

1. INTRODUCTION

Suspension feeding animals obtain their food by trapping suspended particular matter from the water column onto specialized filtering apparatus. Suspension feeders are widely represented among marine invertebrates and some examples are among sponges (Porifera), jellyfish (Cnidaria), bristle worms (Annelida), shrimps (Arthropoda) and bivalves (Mollusca), but also include fishes, birds (flamingos) and mammals (baleen whales). Most of the 30 000 bivalve species described are suspension feeders and their growth relies on the consumption and transformation of phytoplankton and other food sources into bivalve tissue. Spatial and temporal changes in food quality, quantity and availability will therefore influence their growth, metabolism and distribution (Graf et al. 1982; Smaal et al. 1986; Mayzaud et al. 1989).

The grazing activity of dense population of suspension feeding bivalves, either in culture or in natural habitats, have a significant role in the flow of energy and matter in coastal and estuarine ecosystems. These organisms clear vast water volumes of particulate matter and closely couple the benthic and pelagic realms. The bivalves graze on particulate matter as phytoplankton and detritus but also consume micro-zooplankton that compete for the same food resources (Prins and Escaravage 2005; Maar et al. 2007). Grazing directly connects the herbivore to the phytoplankton by changing the population and community structure through size-selective feeding and grazing may induce depletion of phytoplankton and zooplankton (Prins et al. 1998; Maar et al. 2007). The grazing of food particles results in nutrition to the bivalves, while the non assimilated food is egested as biodeposits on the sea bed (faeces and pseudofaeces) and dissolved nutrients (primarily ammonia). The bivalve thereby transform and move nutrients and seston from the pelagic realm to the seabed (Kitchell et al. 1979). The biodeposits degrade into inorganic nutrients aided by microbial activity, and will eventually, in conjunction with the direct excreted inorganic nutrients, support phytoplankton growth and contribute to the overall production of the ecosystem (Prins et al. 1995; Newell 2004).

Dense mussel beds can act as structural habitats for a diverse range of organisms and thereby create local communities (Suchanek 1992). The diversity of the associated invertebrate fauna increases with the size and age of the mussel population and is often linked to the thickness of the bed (Tsuchiya and Nishihira 1985; Tsuchiya and Nishihira 1986). Dense assemblages can exert significant ecological effects including control over phytoplankton, a local influence on

current velocity patterns (Dame 1996) and a dominant role in the flux and cycling of nutrients at the coastal ecosystem scale (Dame 1996; Noren et al. 1999; Haamer and Rodhe 2000; Cranford et al. 2007). When suspension feeder control the abundance of primary producers by their feeding activity it is often depicted as “top down control” (Sterner 1986). In contrast, when nutrient availability (limitation or enrichment) controls primary production by excretion and alteration of nutrient recycling pathways through biodeposition, this is termed “bottom up control” of phytoplankton (Titman 1976; Sommer 1989). Both types of control often occur at the same time. The determination of bivalve contributions to ecosystem energy flow and nutrient cycling and the provision of growth predictions under different environmental conditions are among the main research aims in the field of physiological ecology of suspension feeding bivalves.

Growth predictions of suspension feeding bivalves depend on accurate knowledge of food acquisition rates and the nutritional value of seston obtained under relevant environmental conditions (Bayne 1998). Food acquisition is driven by time dependent environmental forcing, physical constraints of feeding, acclimation capabilities and temporal variation in energy and nutritional demands. An understanding of the food acquisition and utilization is fundamental in the prediction of bivalve growth and the management of shellfish aquaculture (Grant 1996). The requirement to modeling the energetics of suspension feeding bivalves is primarily two sided. First, bivalve aquaculture is increasing and there is a need for growth models to evaluate the production potential (production carrying capacity) of different shellfish growing areas and to optimize farm management towards increased production (Beadman et al. 2002). These models must describe a feeding behavior that is responsive to variations in both the quantity and quality of food in the natural environment (Bayne 1998). Second, estimates of carrying capacity in cultivated areas are being challenged by limitations in the bivalve production caused by density dependent effects (Heral 1993). Bivalve induced seston depletion (Heasman et al. 1998; Ogilvie et al. 2000; Petersen et al. 2008; Strohmeier et al. 2008) relates to a wider interest in bivalve suspension feeder participation (role) in sediment flux, nutrient balance and phytoplankton production in coastal ecosystems (Dame 1996), but also to the management of production, site selection and farm design. A thorough understanding of bivalve eco-physiological behavior and their responses to the environmental forcing is required to achieve these aims.

The competition for space in the coastal zone is increasing and in order to efficiently use the available space the Institute of Marine Research launched a project in 2006 to develop methods for the assessment of carrying capacity in Norwegian aquaculture (CANO, www.imr.no/cano/start). The project constituted three work packages focusing on finfish, bivalves and lobster. This thesis was conducted under the bivalve work package, which aimed "to provide scientific knowledge, competence and modeling capacity that can meet the demands on assessments of carrying capacity of bivalve suspension feeders and to provide practical application of this expertise to develop a culture management system for Norwegian coastal waters". This present study contributed to the project in providing eco-physiological responses of the bivalves to the forcing of low seston conditions. This data was used to improve parameter estimation in models of production and carrying capacity. In addition, the thesis includes data on food availability and condition index in a mussel suspension culture unit in relation to physical flow reduction and mussel grazing. This information was used to develop a mussel farm model of current speed reduction and production capacity according to culture layout/design.

1.1 Ecology and life history of mussels and scallops

The selected suspension feeding bivalves species in this study were the blue mussel *Mytilus edulis* (Fig. 1a) and the great scallop *Pecten maximus* (Fig. 1b). *M. edulis* (Bivalvia; Mytilidae) has a wide distribution extending from subtropical to Arctic regions (Gosling 1992). In the Northern hemisphere it is frequently a dominant animal of rocky shores along both the western and eastern Atlantic coast, extending from the high intertidal to subtidal

Figure 1a. The mussel *Mytilus edulis* in long-line culture. Photo IMR

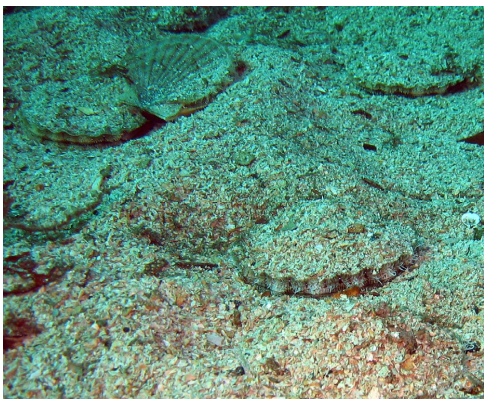

Figure 1b. The scallop *Pecten Maximus* in sea ranching. Photo E. Helland.

regions. *M. edulis* is commonly found from estuarine to fully marine conditions, including the most sheltered habitats to extremely exposed shores. It lives attached by byssus threads on a wide variety of substrates as rock, stones, pebbles, shell, concrete, rope and wood. The upper inter-tidal vertical distribution is usually confined by physical factors while biological factors such as predation and competition primarily set the lower limits (Seed 1969b; Seed 1969a; Paine 1976; Suchanek 1992). In Norwegian waters *M. edulis* may become reproductive during the first year but gametes are normally not released until the second reproductive season (Duinker et al. 2008). The major spawning event is during the spring and summer season. *M. edulis* reaches market size during the second or third year at 5-6 cm shell length.

Compared to *M. edulis*, the distribution of *P. maximus* is limited, with individuals confined from the south of Lofoten islands in Northern Norway to the Iberian Peninsula, including the Azores, the Canary Islands, Madeira and off West Africa (Mason 1983; Ansell 1991). It is abundant below the low water mark down to approximately 200 m depth and is normally observed in shallow depressions on a seabed consisting of firm sand, shell sand or occasionally on muddy sand. *P. maximus* may occur at high densities from 10 to 60 meters depth along the Norwegian coastline, however the distribution of this species is invariably patchy. It is a stenohaline species with limited tolerance to low temperature (Strand et al. 1993). *P. maximus* is a functional hermaphrodite and becomes sexually mature during the second year, with spawning in Norwegian water being reported during spring and summer (Strand and Nylund 1991b; Strohmeier et al. 2000). Wild harvested *P. maximus* normally reach market size at 10 cm shell height within the fourth or fifth year. Initial results from sea ranching indicate an additional year or two is required to achieve this size (personal observation). Scallops are among the few bivalves species with the ability to swim. The swimming behavior is primarily an escape response to predation but may also be used to select habitat and to recess *P. maximus* in the sediment (Mason 1983; Wilkens 1991). This leaves the upper valve (e.g left valve) flush/level with the sediment surface.

1.2 Food and its availability to suspension feeders

The potential food for suspension feeding bivalves is phytoplankton, detritus, bacteria, micro-zooplankton and dissolved organic material (DOM). Plankton and inorganic and organic particulate matter in suspension are collectively termed the seston. Food availability primarily controls the growth of suspension feeding bivalves (Winter 1978; Bayne and Newell 1983;

Soniat and Ray 1985; Berg and Newell 1986) and is affected by seston concentration and composition as well as the transport rate (Frechette and Bourget 1985b; Cranford and Hill 1999). The seston is transported by the water currents and may be regular as when forced by tidal currents or irregular as when forced by wind or fresh water runoff. Seston concentration in coastal waters can vary on short spatially and temporal scales with distinct changes in the concentration, composition and nutritional value of the seston (Fegley et al. 1992; Danovaro and Fabiano 1997; Cranford and Hill 1999). In temperate water, long term changes in seston abundance and composition are driven by seasonal cycles in primary productivity, while short-term variability is influenced by phytoplankton blooms (Cranford et al. 2005), horizontal and vertical phytoplankton patchiness and tidal or storm induced re-suspension of sediment (Cranford et al. 1998). Seston in shallow bays and estuaries susceptible to strong re-suspension events typically have reduced food quality caused by inorganic dilution. Such inorganic dilution has been reported to both enhance (Kiorboe et al. 1980; Kiorboe and Mohlenberg 1981; Bayne et al. 1987) and reduce or inhibit bivalve growth (Bricelj et al. 1984). Suspension culture habitats situated high above the seabed (e.g deep fjords) are not susceptible to re-suspended sediments and the bivalves are more likely to graze on seston dominated by phytoplankton.

The seston concentration shows large temporal and spatial variation at coastal culture sites in many regions of the world (Saxby 2002). The range of seston quantity and quality observed in most studies of bivalve feeding commonly vary from 3 to 100 mg suspended particulate matter (SPM) L^{-1} of which 5-80 % may be organic (Bayne and Hawkins 1990). These SPM values are considerably higher compared to the seston quantities found in many regions where bivalves reside, including oligotrophic environments. In order to contrast these food environments the term “low seston environment” have been assigned to coastal regions that typically show SPM and chlorophyll *a* quantities below 1.0 mg L^{-1} and 1.5 µg L^{-1} (excluding spring phytoplankton blooms), as such quantities represent lower seston values than reported by Bayne and Hawkins (1990).

Bivalve farming is typically an extensive form of aquaculture that relies on natural seston for feeding. In Norway, *M. edulis* and *P. maximus* are normally cultured in different habitats. *M. edulis* are farmed close to the surface (0-10 m depth) on suspended ropes hanging down from long-lines. Suspension culture provides feeding in the pelagic realm with water renewal in three dimensions. Scallops are typically farmed on the seabed where they feed within the

benthic boundary-layer, which allows them to utilize the epibenthic detritus layer and benthic phytoplankton (Chauvaud et al. 2001). In addition, modest valve clapping may resuspend the sediment surface and this trait may enhance food availability (Davis and Marshall 1961). Due to the different environmental conditions experienced by cultured *M. edulis* and *P. maximus*, the food supply will differ both in the amount and composition of seston delivered by lateral advection (Macdonald 1986; Claereboudt et al. 1994).

The nutritive value of the seston varies both temporally and spatially in response to physical and biological factors (Berg and Newell 1986; Danovaro and Fabiano 1997). The nutritional quality of different particulate food sources for scallops, including cultured phytoplankton, kelp detritus and re-suspended sediment of scallop diet, has been studied in the laboratory for *Placopecten magellanicus* (Cranford and Grant 1990; Grant and Cranford 1991). Within these treatments the results signified phytoplankton as the highest quality food source, but detritus could contribute to energy acquisition and growth when phytoplankton was less abundant. Shumway et al. (1987) studied the seasonal variation in the gut content of *P. magellianicus*. Besides both pelagic and benthic phytoplankton (size 10-350 μm) the gut contained considerable amounts of detritus and bacteria. The importance of phytoplankton as a food source is also reported for *Patinopecten yessoensis,* where diatoms and heterotrophic flagellates were key constitutes of the diet along with ciliates and invertebrate larvae, while detritus was found to be insignificant (Silina and Zhukova 2007b; Silina and Zhukova 2007a).

Although phytoplankton are frequently reported as the primary food source for bivalves, some species can be harmful or toxic. High concentrations of the diatom *Rhizosolenia delicatula* and *Ceratulina pelagica* are suspected to cause gill clogging and cessation of growth in *P. maximus* (Chauvaud et al. 1998; Lorrain et al. 2000) due to reduced feeding and respiration abilities. Numerous other effects including an escape response in scallops (swimming), strongly enhanced mucus production, atrophy and necrosis of the digestive gland absorptive cells, dead hemocytes and mass mortality (Shumway and Cucci 1987; Gainey and Shumway 1988; Shumway et al. 2006; Wikfors et al. 2008) are associated with the phytoplankton species *Prorocentrum minimum*, *Pfiesteria* sp., *Prymnesium* sp., *Gyrodinium* sp. and *Alexandrium tamarense*.

Whether bivalves can efficiently utilize detritus as a food source seems to depend on the nutritional composition, the associated feeding behavior and digestive response to the detritus.

Detritus of sea grass, marsh grass and macroalgae low in essential nutrients (i.e. low nitrogen content) have resulted in a negative energy balance in *P. magellanicus*, caused in part by reduced feeding rates and net absorption efficiency (Grant and Cranford 1991). On the other hand various bivalves may grow on macrophyte detritus (Newell and Langdon 1986; Crosby et al. 1989), and the marsh-grass (*Spartina alterniflora*) can constitute 30-50% of the carbon and sulfur in the tissue of *Aulacomya ater* (Stuart 1982). Some bivalves have adapted enzyme systems to digest refractory POM and may shift the digestive physiology in responds to dietary components (Kreeger and Newell 2001). Further research on digestive enzymes may provide valuable information on the digestive function according to the nutritional quality of seston (Ibarrola et al. 1998).

Particulate organic matter (POM) provides the substratum for bacterial processes and the degradation of detritus by bacteria is a fundamental step for the transfer of energy to higher trophic levels (Crosby et al. 1990; Danovaro and Fabiano 1997). Bacteria utilize organic matter to grow, but at the same time they convert refractory organic detritus into bacterial biomass. This process increases the protein content (lower C:N ratio) and enhances the POM quality (Abreu et al. 1992). The bacterial-plankton have a high nutritional value (C:N ~ 3.5) compared to phytoplankton (C:N ~ 6.6) and bacteria concentration can be high in eutrophic estuaries, kelp beds and mashes (Corre and Prieur 1990; Langdon and Newell 1990). However, the bacteria size are typically too small (0.3 to 1 μm) to be retained on most bivalve gills, unless they are aggregated or associated with particles.

Bivalves can actively transport DOM and free amino acids (FAA) over the bivalve gill and utilize it as a nutritional supplement (Stewart and Bamford 1975; Manahan et al. 1982; Roditi et al. 2000). Manahan (1983) estimated that 34% of the metabolic cost could be covered by the uptake of FAA. This number has later been reduced to about 10% (Hawkins and Bayne 1992). In an oligotrophic fresh water system, the absorption of C^{14} labeled carbon by the zebra mussel (*Dreissena polymorpha*) indicated that 50% of the carbon demand could be covered by dissolved organic carbon (Roditi et al. 2000). Albeit the uncertainty, this suggests that DOM can serve as a potential energy source for bivalves and perhaps of more importance when other diets are scarce. Although the food ration has been recognized as the major factor regulating bivalve growth and production, there is still a lack of knowledge on bivalve food resources and their nutritional value at various time of the year.

1.3 Suspension feeding and physiology

Suspension feeding bivalves use the gills in particle capture. The gills have become greatly enlarged during evolution to handle their additional function in feeding. Both species included in this study are active suspension feeders, requiring the individual to use its own energy to transport seawater across the filtration apparatus where particle capture is facilitated. Figure 2 shows a schematic representation of the physiological feeding processes in a suspension feeding bivalve. The first step of feeding is to transport seawater through the mantle cavity and to capture particles onto the gills or labial palps (Ward and Shumway 2004). The feeding current is created by coordinated movements of lateral cilia situated on the gill filaments. The amount of food captured is dependent on the volume of water transported across the gills and the efficiency with which particles are retained on the gills. Not all sizes of food particles are acquirable due to the different retention efficiency of particles on the bivalve gill (Ward and Shumway 2004). The captured particles are transported in tracts towards the mouth in either a cohesive mucus string (ventral tract) or less cohesive mucus slurry (dorsal) (Beninger et al. 1992; Beninger et al. 1993; Ward and Shumway 2004). At low seston quantities virtually all particles cleared out of suspension are ingested (Hawkins et al. 1999), but at higher seston quantities pre-ingestive selection occurs by preferential capture of particles on the gills or by rejecting pseudofaeces from either the gills or/and labial palps (Ward and Shumway 2004). At relatively high seston quantities (e.g ~ 3-6 mg SPM L^{-1} for *M. edulis*, depending on body size (Widdows et al. 1979) and ~ 10 mg SPM L^{-1} for scallops (Macdonald and Ward 1994), the surplus material is rejected prior to ingestion.

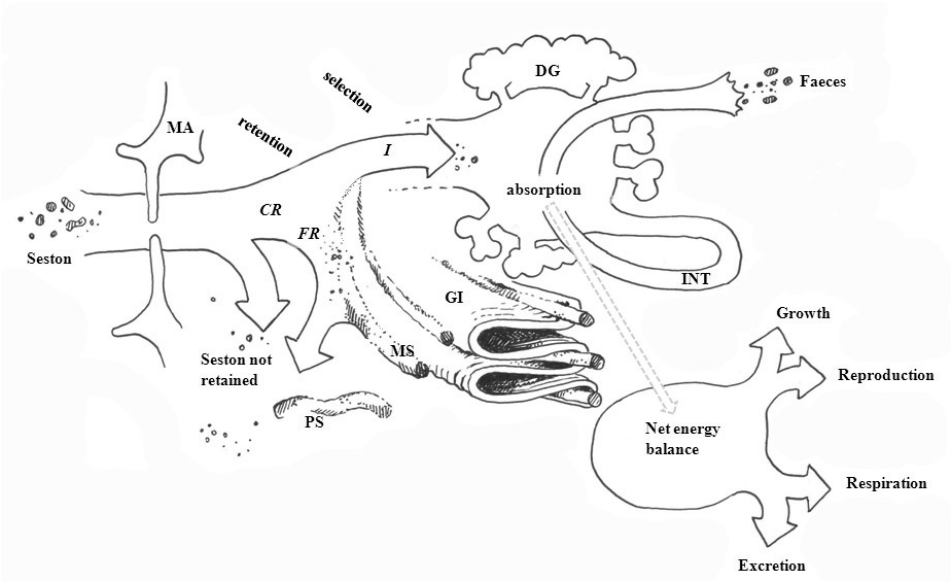

Figure 2. Schematic drawing of feeding and physiological processes in suspension feeding bivalves. The seston enters the bivalve through an opening in the mantle tissue (MA). Particles are cleared out of suspension as the feeding current passes the gills (GI) in mucus strings (MS) or slurry. The clearance rate (*CR*) is the volume of water cleared from particles per unit time. The retention efficiency is the efficiency by which particles are captured onto the gills. The filtration rate (*FR*) is the amount of material retained on the gills per unit time. The captured material may be ingested or rejected as pseudofaces (PS), i.e. bivalves may select from the captured particles with a certain efficiency = selection efficiency. The ingestion rate (*I*) is the amount of material ingested per unit time. The efficiency in which ingested seston is absorbed in the digestive gland (DG) and the intestine (INT) is net absorption efficiency, while the non digested material is expelled as faeces. Absorbed material is metabolized and used in growth and maintenance. Respiration represents an energy loss from oxidized carbon while excretion represents loss of nitrogen from protein metabolism. The net energy balance is the result of energy acquisition – expenditure and surplus energy may be used in growth and/or reproduction. Drawing by Stein Mortensen.

The ingested food is transported through the oesophagus by the ciliated epithelial lining to the stomach, where it is mechanically disintegrated by the crystalline style rotating against the gastric shield. The crystalline style, the stomach wall and the gastric shield releases enzymes that contribute in chemical degradation and extracellular digestion in the stomach (Reid 1968; Mathers 1973). The stomach content is transported to the digestive diverticula or gut for further intracellular digestion and absorption (Morton 1983). The food particles are absorbed in the digestive diverticula by endocytosis or pinocytosis for intracellular degradation in digestive cells, aided by the lysosomal system (Moore et al. 2007). Non digestive material is expelled from the cells as residual bodies and excreted via the intestine. Particles from the stomach and remnant material from the digestive gland pass into the intestine where it can be

engulfed by haemocytes or further degraded by enzymes (Lepennec et al. 1991). The assimilated nutrients are utilized in growth, respiration and excretion. The faeces are expelled at the anus and exit through the exhalent opening of the mantle.

Suspension feeding bivalves cope (i.e. acclimation and compensation) with the high variation in diet quantity and quality occurring in nature (section 1.2), by actively adjusting varies component of their feeding and digestion physiology (Fig. 2). The ability of suspension feeding bivalves to control clearance rate primarily determines food acquisition (Hawkins et al. 1999; Gardner and Thompson 2001; Hawkins et al. 2001; Cranford et al. 2005), and individual bivalves feeding on natural seston appear to vary feeding activity continuously (Frechette and Bourget 1987). Suspension feeding bivalves exposed to increasing seston concentrations may reduce the time spent pumping (discontinuous feeding behavior), reduce clearance rate and/or increase the amount of material rejected in pseudofaeces (Foster-Smith 1975; Foster-Smith 1976). Water pumping and clearance rate has been reported to be controlled by the activity of the lateral cilia, valve opening and the exhalant siphon area (Jorgensen et al. 1988; Jorgensen and Ockelmann 1991; Newell et al. 2001). Recently, the relationships between clearance rate, valve opening and exhalant siphon area have been questioned (Frank et al. 2007; MacDonald and Ward 2009). In order to initiate suspension feeding, the food concentration must exceed a threshold value. The seston concentrations at which mussels are reported to start feeding come from laboratory experiments using artificial diets (Riisgard and Randlov 1981; Newell et al. 2001; Riisgard et al. 2003b; Riisgard et al. 2006) and from field studies through observation of valve gape (Dolmer 2000b; Dolmer 2000a; Riisgard et al. 2006; Saurel et al. 2007). The threshold concentration for feeding has been reported as: (1) 0.4 – 0.5 µg Chl *a* L^{-1} (Dolmer 2000b), (2) 1500 cells cm^{-3} *Phaeodactylum tricornutum* (equivalent to 1 µg Chl *a* L^{-1}; (Riisgard and Randlov 1981), (3) 0.5 to 1.5 mm^3 particle volume L^{-1} (Newell et al. 2001), (4) 630 *Rhodomonas* sp. cells cm^{-3} (approximately 0.5 µg Chl *a* L^{-1}; (Riisgard et al. 2003a; Riisgard et al. 2006), and (5) approximately 0.9 µg Chl *a* L^{-1} (Riisgard et al. 2006). Together these studies indicate that bivalves start suspension feeding at Chl *a* levels between 0.5 to 0.9 µg L^{-1}. Above this concentration both mussels and scallops have shown a unimodal clearance rate response to increasing seston quantities/volume (Hawkins et al. 1999; Hawkins et al. 2001).

Many suspension feeding bivalves retain 100% of particles above 3-4 µm. The retention efficiencies of particles decreases with smaller particle to 35–90 % for 2 µm particles

(Mohlenberg and Riisgard 1978). Owing to the differences in gill morphology (the underdeveloped latero-frontal cirri on the gill filament), the investigated members of the Pectinidae efficiently retain slightly larger particle sizes (e.g 5-7 μm) (Mohlenberg and Riisgard 1978; Palmer and Williams 1980; Riisgard 1998). Particle retention efficiency might in addition to particle size depend on particle shape, motility, density and chemical clues (Hawkins and Bayne 1992).

Suspension feeding bivalves may increase the nutritional value of the seston ingested by preferential capture of particles on the gills or by rejecting pseudofaeces from either the gills or/and labial palps (Ward and Shumway 2004). Particle selection through pseudofaeces production has been demonstrated on bivalves provided cultured algae, mixtures of cultured algae and sediments and assemblages of natural seston (Kiorboe et al. 1980; Newell and Jordan 1983; Shumway et al. 1985; Cranford and Gordon 1992; Macdonald and Ward 1994; Shumway et al. 1997; Bacon et al. 1998). The efficiency of particle selection appears variable both within and among species, and it is likely related to palp size and seston composition (Kiorboe and Mohlenberg 1981; Iglesias et al. 1992; Urrutia et al. 1996).

Selection of food items also occurs in the stomach where ridges and grooves situated in ciliary tracts act as sorting areas and low quality particles (i.e. sand grains etc.) are segregated out and channeled into the intestine along a rejection groove on the floor of the stomach (Gosling 2003). Selection in the gut or digestive gland is not well known but it has been indicated that some bivalves can differentiate between particles in the gut and preferentially digest particles according to their nutritional value (Bricelj et al. 1984; Lopez and Levinton 1987). Selection may be due to longer gut retention time for certain particles (Cranford et al. 1998; Brillant and MacDonald 2002; Brillant and MacDonald 2003), to increase extracellular digestion time or by redirecting particles to the digestive gland for intracellular digestion. The digestive activity is regulated and coupled to the ingested food quantity and there is a positive correlation between the quantity of food ingested and the stomach and gut passage time (Bayne et al. 1984). This relationship influences the degradation efficiency and absorption of nutrients from the ingested food (Rouillon and Navarro 2003; Gueguen et al. 2008). The morphological constraints of gut volume and the time required to digest food can limit the amount of food ingested (Hawkins et al. 2001).

Absorption efficiency in both field and laboratory studies are reported to consistently increase with the quality of seston, and absorption efficiency seems independent on whether the organic fraction or the concentration of nitrogen or carbon (when determined) were used as an indicator of diet quality (Vahl 1980; Bayne et al. 1987; Cranford and Grant 1990; Cranford 1995; Grant et al. 1997; Cranford et al. 1998; Hawkins et al. 1998b; MacDonald et al. 1998). However, high absorption efficiencies are not sufficient to support growth as the absorbed food may lack essential nutrients (Langdon and Waldock 1981; Grant and Cranford 1991). Altogether this suggests that bivalves have several physiological responses to the available food and may regulate food acquisition according to their needs (Hawkins and Bayne 1992; Bayne 1998).

1.4 Aquaculture in low seston environment

Bivalves are considered as high-quality food and aquaculture production has great commercial value which is reflected in the large volumes cultured worldwide (1.256×10^6 tonnes marine molluscs in 2006 (Anon 2006)). The demand is also increasing. Most of the bivalve production occurs in Asia, with China as the largest producer. *M. edulis* and *P. maximus* represent currently the largest commercial potential in Norwegian coastal waters but adds little to the total yield with an annual production and harvest of approximately 3.7×10^3 in 2006 (Anon 2009) and 1×10^3 tonnes respectively. The Norwegian coast is long and contains large sheltered areas that are potentially suitable for farming. However, the anticipated expansion and export volumes have not been realized, in part because of low meat yield, probably related to overcrowded stocks and an oligotrophic environment (Strohmeier et al. 2008).

The phytoplankton concentration in Norwegian fjords rarely exceeds 1.5 µg Chl *a* L^{-1} (except during phytoplankton blooms) (Erga 1989; Frette et al. 2004) due to nutrient limitation (Paasche and Erga 1988) and the fjords are too deep for resuspended sediments to increase seston concentration in shallow water suspension culture. In contrast, many international bivalve cultivation sites take advantage of locally high phytoplankton biomass and sediment resuspension. Some examples include the Ria de Arousa with 4-12 µg Chl *a* L^{-1} (Figueiras et al. 2002), Benguela Bay with 8 µg Chl *a* L^{-1} (Pitcher and Calder 1998), the Oosterschelde with 7.5 µg Chl *a* L^{-1}, Marennes-Oléron Bay with 4-22 µg Chl *a* L^{-1} and Chesapeake Bay with 6.9 µg Chl *a* L^{-1} (Dame and Prins 1998). The low seston concentration in the Norwegian

farming environment is a major concern for two reasons. First, mussels are reported to stop suspension feeding when the Chl *a* quantities decreases below 0.5 to 0.9 μg L^{-1} (see Section 1.3). Second, the net zero energy balance for the green lipped mussel (*Perna canaliculus*) has been estimated at ~ 0.9 μg Chl *a* L^{-1} (Hawkins et al. 1999). If these threshold values are geographically universal, they will have severe consequences for the production capacity of bivalves in low seston environments.

Suspension-feeding bivalves have a remarkable capacity to filter the water column and to deplete the water of seston (Navarro et al. 1991) and in dense cultures they may be food limited through their collective impact on the seston (Grant 1996; Heasman et al. 1998). The degree of seston depletion mainly depends on the rate at which the seston is replaced by lateral advection (Roegner 1998; Grant and Bacher 2001) and phytoplankton growth, but it also relates to ambient seston quantity and quality, bivalve physiology, stocking density and cultivation unit layout (Section 3.4). In this text, seston depletion refers to any measureable reduction in seston quantity that is caused by the retention of particles by bivalve suspension feeders. Seston depletion does thereby not necessarily imply seston limitation and a negative impact on growth, but in severe cases overcrowding may depress bivalve growth rate and increase mortality (Grant et al. 1993). Given the negative consequences on shellfish production from overstocking there has been a large focus on the prediction of carrying capacity ranging from the individual bivalve, to farm units and to the full ecosystem range (Beadman et al. 2002).

Production carrying capacity at the farm level is highly site specific as the magnitude and scale of food depletion depends on operational (husbandry) and regional (external and internal food replenishment features) characteristics. In order to understand the mechanisms of growth and thereby to estimate carrying capacity we need knowledge of the dynamics of the food supply in the cultivation environment but also the processing and conversion of food into bivalve tissue, mediated by the physiological energetics of the culture species (Grant 1996). There is a lack of knowledge in the bivalve physiological feeding responses to low seston concentrations, but they are known to have a high capacity to adapt to the local environment by altering their feeding behavior by a range of regulatory processes that respond to fluctuations in seston availability and quality (Bayne 1998; Ward and Shumway 2004). To understand the functional feeding physiology of bivalves to the range of dietary conditions in nature, it is necessary to expose bivalves to a wide range of feeding conditions and include the

lower extremes of naturally occurring concentrations (Hawkins et al. 1999). Knowledge of growth and feeding physiology to bivalves in oligotrophic environments or at high culture densities is required to understand and predict shellfish distribution, production and survivorship in oligotrophic environments. This knowledge is particularly relevant to bivalve aquaculture, both to optimise site selection and to estimate production and ecological carrying capacity.

2. OBJECTIVES OF THE STUDY

The main objective was to study the functional feeding responses of two commercially important bivalve species (*Mytilus edulis and Pecten maximus*) to the dietary conditions in a natural low seston environment. Further objectives were to determine the net zero growth and net zero energy balance of the bivalves to help facilitate growth predictions. On a cultivation unit scale, the aim was to describe physical and biological components of seston depletion processes in long-line suspension culture, to optimize cultivation unit design, carrying capacity assessment and site selection. The objectives of the papers were to:

- **Paper I**: Test present hypothesis on clearance rate responses of scallops and mussels at natural low and diluted seston quantities, including levels above and below the reported threshold concentration for cessation of feeding. Further objectives were to investigate the functional feeding response and to seasonally variable environmental conditions and to provide predictive relations for scallops and mussels clearance rate responses at seston levels that are ecologically relevant in low seston environments.
- **Paper II:** Investigate seasonal variations in tissue growth and to determine the net zero energy balance of the bivalves at natural low and diluted seston concentrations.
- **Paper III:** Describe the variation in water current pattern, phytoplankton concentration and bivalve condition index in a *M. edulis* long-line unit of a relatively high stocking density.
- **Paper IV:** Model the current speed reduction and production carrying capacity according to the structural design of long-line mussel (*M. edulis*) units.

3. GENERAL DISCUSSION

The conversion of primary production into bivalve biomass is the energetic basis of aquaculture. Numerous papers report that the growth of suspension feeding bivalves is largely controlled by food availability (Winter 1978; Widdows et al. 1979; Incze et al. 1980; Bayne and Newell 1983; Rodhouse et al. 1984; Frechette and Bourget 1985a; Macdonald and Thompson 1985; Brown 1988; Thompson and Nichols 1988) and temporal and spatial variations in the physiological components of growth are mediated by variations in seston abundance and composition (Bayne and Widdows 1978; Cranford and Hargrave 1994; Navarro and Thompson 1995; Smaal et al. 1997; Cranford et al. 1998; Cranford and Hill 1999; Cranford et al. 2005; MacDonald and Ward 2009). The relationships between growth and temperature, food availability and composition are not well understood (Grant 1996; Cranford and Hill 1999). The interrelationship between temperature and food complicates the interpretation of causality for observed growth changes. This lack of causality has been attributed to growth being the sum total of several energy budget terms that respond differently, and sometimes non-linearly, to environmental changes. An understanding of the complex interplay that exist between the physiological processes controlling food utilization is necessary to predict bivalve growth (Grant 1996; Bayne 1998), stocking density, optimal farm design and localization, and to avoid seston depletion.

3.1 Feeding behavior at low seston quantities

Bivalve feeding responses to environmental changes have been extensively studied (Bayne 1998; Cranford and Hill 1999; Hawkins et al. 1999; Hawkins et al. 2001; Cranford et al. 2005), however, there is still a lack of knowledge of feeding processes in relation to natural low seston concentrations. The clearance rate is likely the most important physiological trait of suspension-feeding shellfish. This rate determines the grazing rate and it modulates energy acquisition (Hawkins et al. 1999; Gardner and Thompson 2001; Hawkins et al. 2001; Cranford et al. 2005). The available information on clearance rate responses is obtained on bivalves from regions with relatively high seston levels. Several studies report that the food quantity must exceed a threshold value of 0.5 to 0.9 µg Chl *a* L^{-1} to initiate suspension feeding (see section 1.3). Above this concentration, both mussel and scallop have shown a unimodal clearance rate response to increasing seston quantities/volume (Hawkins et al. 1999; Hawkins et al. 2001).

The seasonal clearance rate responses of *P. maximus* and *M. edulis* to natural low (treatment 1) and through successively diluted seston concentrations with deep water (treatment 4) show that both species consistently filter-feed at intermediate to high rates at seston quantities well below the alleged threshold concentration reported for cessation of feeding (Paper I). In fact, the study did not detect a seston threshold concentration in which the bivalves ceased feeding, even when using Chl *a* concentrations as low as 0.01 µg L^{-1}. At ambient low seston concentrations virtually all bivalves cleared particles. On the contrary, most of the scallops that ceased suspension feeding did so during the period of high Chl *a* quantities during late winter and spring blooms. The mean clearance rate response obtained in the seasonal study is consistent with the mean cohort response reported in the short-term study (Paper I), however some individual bivalves showed short-term variation (hours) in clearance rate.

The clearance rates obtained in Paper I typically reflected the maximal capacity which is uncommon for studies utilizing natural seston diets (Widdows et al. 1979; Macdonald and Thompson 1986; Bayne et al. 1987; Cranford and Grant 1990; Cranford and Gordon 1992; Smaal et al. 1997; Cranford et al. 1998; Cranford and Hill 1999; Pilditch and Grant 1999b; Petersen et al. 2004; Cranford et al. 2005; Kittner and Riisgard 2005; MacDonald and Ward 2009). In an ongoing review of 61 clearance rate studies of Mytilid species, the mean clearance rate averaged 2.6 L g^{-1} h^{-1} and maximal rates were at approximately 5 L g^{-1} h^{-1} (Cranford, in preparation). Maximal clearance rates are mostly reported for bivalves feeding under closely controlled laboratory studies employing one or a few species of cultured phytoplankton (Riisgard and Randlov 1981; Riisgard et al. 2003b). The mechanisms for the variability in clearance rate between studies and the high feeding rates observed can be related to the high diet quality and morphological plasticity of the foraging apparatus (Piersma and Lindstrøm 1997; Piersma and Drent 2003). Flexibility in the size of gills and palps to natural turbidity has been demonstrated for suspension feeding bivalves (Theisen 1982; Payne et al. 1995a; Payne et al. 1995b; Barille et al. 2000). These previous findings indicate smaller gills (and larger palps) at turbid sites, which would correspond to large gills and thereby high feeding rates in the seston environment studied in Paper I.

Functional feeding curves of suspension feeding bivalves are typically given as plots of food concentration against clearance or ingestion as observed in feeding experiments (Widdows et al. 1979; Bayne and Newell 1983) and modeled as saturation responses (Vanharen and Kooijman 1993; Pouvreau et al. 2006; Rosland et al. *In press*). The functional feeding curves

shown in Paper I were based on a modest variation in seston quantity compared to the wide range of seston characteristics reported previously on bivalve feeding behavior. Hawkins (1999) studied feeding responses for the green-lipped mussel *P. canaliculus* over a range of seston availability wider than previously studied in any bivalve species. This mussel shows a broad optimal range of feeding conditions over which maximal rates of food ingestion and absorption were achieved at the lowest seston concentrations studied (1-2 µg Chl *a* L^{-1}). Within the low seston quantities provided in the present study, *P. maximus* showed a curvilinear response to changes in food concentration (Fig. 3). Clearance rate was already intermediate at 0.1 µg Chl *a* L^{-1}, increased to maximal values at 0.4 µg Chl L^{-1} and decreased above this concentration. This clearance rate response pattern is in accordance with Hawkins et al. (2001) who predicted that clearance rate of the scallop *Chlamys farreri* increases with food availability to a maximal value and then declines with further increases in Chl *a*. However, maximal clearance rate and the following decline occurred at substantially lower seston quantities in the present study (response curve skewed to left, Paper I). This finding shows that *P. maximus* regulate clearance rate in response to relatively small changes in phytoplankton quantity, a response that significantly can enhance energy acquisition.

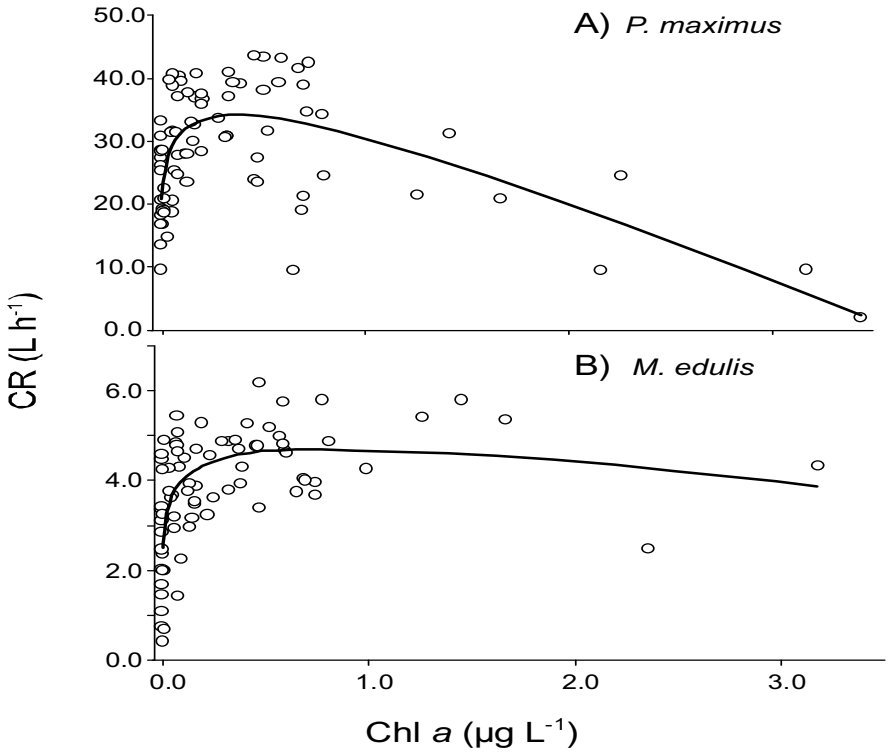

Figure 3. Mean clearance rate (*CR*) data for *P. maximus* (A) and *M. edulis* (B) at increasing chlorophyll *a* concentrations (Figure from Paper I). Each point in the figure represents the mean value of 18 individual CR measurements. All data from four seston treatments are included.

The feeding response in *M. edulis* was also intermediate at the lowest Chl *a* quantities provided (Fig. 3). The clearance rate increased rapidly to maximal values at about 0.2 µg Chl *a* L^{-1}, but contrary to *P. maximus,* the *M. edulis* clearance rate did not decline markedly at the higher seston quantities given. *M. edulis* have previously shown a constant clearance rate over a large range of seston quantities (Foster-Smith 1975; Smaal et al. 1997), and the clearance rate tend to be less responsive to fluctuations in suspended food particles compared to scallops (MacDonald and Ward 2009), but may decrease at high particle concentrations (> 50 mg SPM L^{-1}) (Widdows et al. 1979).

Paper I represent a revised view of suspension-feeding behavior at an environmental extreme that includes a large fraction of the biogeographical distribution of bivalve mollusks. The results show that these bivalves are not limited in their distribution or in aquaculture by the ability to clear particles out of suspension. Both *P. maximus* and *M. edulis* showed an

exploiter strategy to low seston concentrations by avoiding cessation of feeding, responding rapidly to minor increases in seston quantities (i.e from 0 to 0.4 µg Chl *a* L^{-1}) and typically maintaining a high clearance rate. The ultimate cause of this feeding behavior is likely the need to acquire energy at lower food concentrations compared to bivalves situated in higher seston environments. Results from Paper I have been used to improve parameter estimation for mussel growth models applied in a low seston environment (Rosland et al. *In press*) and will be used in the further development of models to study seston depletion in bivalve culture (Section 3.4).

Northern hemisphere environments typically show high food concentration at low temperatures during the spring bloom (Loo 1992; Cranford et al. 2005); Paper I). The reported effect of temperature on feeding rate within the temperature-tolerance range is quite diverging. One view points to maximal feeding rates being approximately linearly related to temperature (Jorgensen et al. 1990b). This view emphasis that the lateral cilia are under both the influence of seawater viscosity, which is physically controlled by temperature, and the effect of temperature on biochemical reactions (Riisgard and Larsen 2007). On the other hand, several reports point to thermal compensation of feeding rates on acclimated bivalves (Widdows and Bayne 1971; Widdows 1976; Smaal et al. 1997; Cranford and Hill 1999; Cranford et al. 2005) and both scallops and mussels have shown rather stable feeding rates despite changes in sea water temperature (Bayne et al. 1976; Smaal et al. 1997). Bivalves are also shown to clear and ingest particles at high rates at temperatures as low as -1°C (Loo 1992; Sejr et al. 2004; Cranford et al. 2005).

Although the seasonal *P. maximus* clearance rate responses reported in Paper I were correlated to the ambient changes in temperature, this statistical relationship was inconsistent across seston treatments and did not hold up during the spring bloom, in which clearance rate was strongly negatively correlated to Chl *a* quantity and not to temperature. The changes in food quantity during the spring bloom appeared to stimulate *P. maximus* clearance rate responses to a greater degree than changes in ambient temperature. This is also supported by a lack of acute change in clearance rate during a 5.4°C temperature decrease over a three day period in December. There was no correlation between clearance rate in *M. edulis* and temperature. The lack of correlation between temperature (from 19.6 to 4.6°C) and *M. edulis* clearance rate suggest that the mussels acclimated to the temperature changes, and the study supports that *M. edulis* are capable of maintaining thermal independence in feeding

performance over a wide range of temperatures (Widdows 1976; Smaal et al. 1997; Cranford and Hill 1999). As intermediate to maximum clearance rate for both species were recorded over the full range of ambient temperatures the effect of sea water viscosity on feeding rates seems marginal. Pumping activity requires little energy compared to total metabolic costs (Jorgensen et al. 1990a; Willows 1992) and it appears that bivalves that are fully acclimatized to low seston conditions are able to offset feeding costs by maximizing ingestion of dilute diets.

3.2 Tissue growth at low seston quantities

In order for bivalves to grow tissue mass, the energy obtained from the food must exceed the metabolic expenditures. The information on the seston concentration needed to achieve a net zero growth or energy balance is scarce. Hickman et al. (1991) reported a significant decrease in condition index for *P. canaliculus* at seston quantity below 200 µg C L^{-1} and Page and Hubbard (1987) reported rather stable somatic and reproductive tissue weights for *M. edulis* during a three month period at a seston quantity of ~ 200 µg POC L^{-1} (or ~ 1 µg Chl *a* L^{-1}). This value is comparable with the estimated net zero energy balance for *P. canaliculus* at a Chl *a* availability of ~ 0.9 µg L^{-1} (Hawkins et al. 1999). The net zero energy balance reported in Paper II was at seston concentrations of ~ 80 µg POC L^{-1} and ~ 0.4 µg Chl *a* L^{-1}. These threshold values are less than half those reported above and are linked to the lack of cessation in feeding and the high feeding rates detected at low seston concentrations (Paper I). The low net energy balance and the positive tissue growth detected in the present study indicate that *P. maximus* and *M. edulis* grow at much lower seston concentrations than previously assumed.

The *P. maximus* growth rate to increasing food quantity appeared linear at increasing SPM, POM and POC concentrations (Fig. 4), suggesting that the energy obtained from the seston increased linearly and that the growth rate would increase at higher seston quantities. However, asymptotic growth was indicated at increasing Chl *a* concentrations. This suggest that the nutritional value (e.g. utilizable fraction) of phytoplankton (measured as Chl *a*) is nonlinearly related to its concentration (i.e. the utilizable fraction at high Chl *a* concentration is poor compared to low concentration).

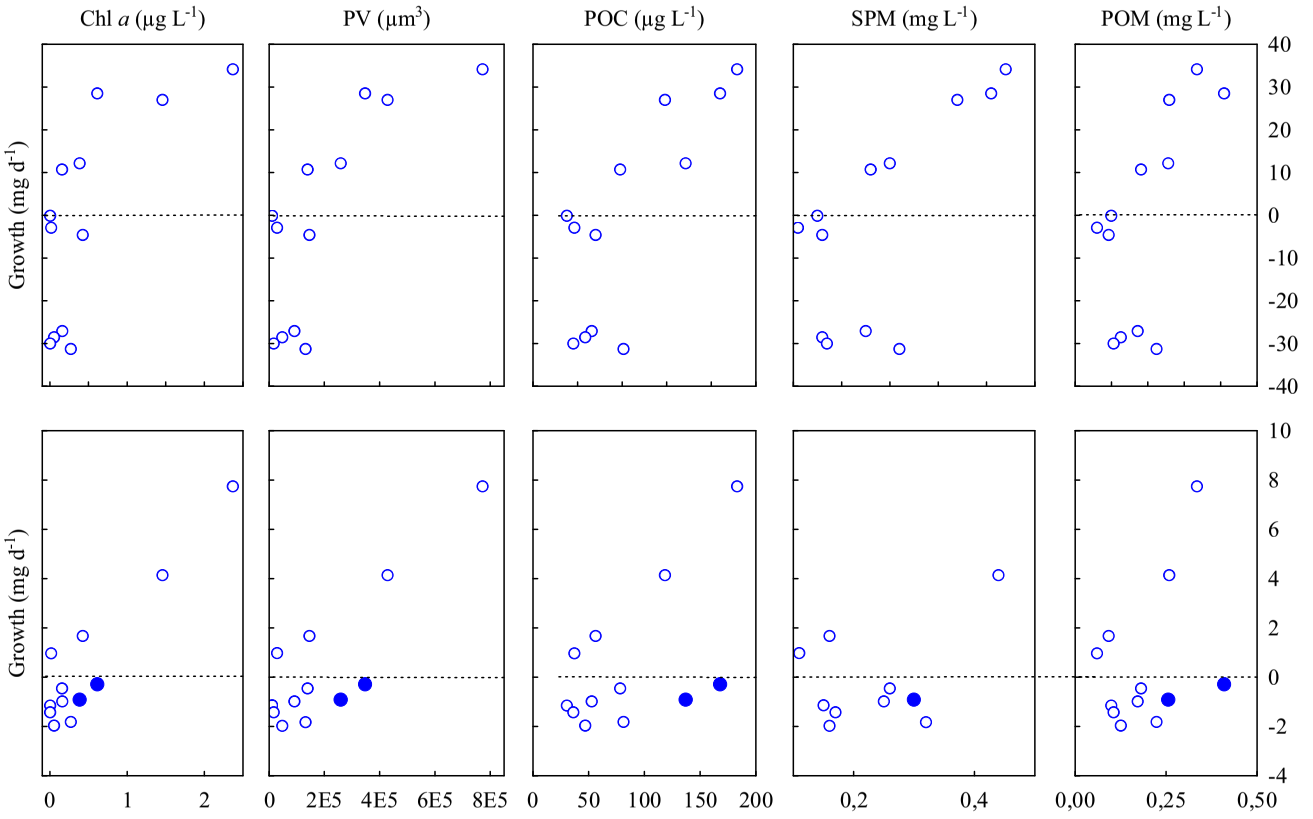

Figure 4. Relationship between the estimated dry flesh weight growth (mg d^{-1}) of *P. maximus* (top panels) and *M. edulis* (bottom panels) and different measures of food concentration (Figure from Paper II). Growth data are mean values from autumn, winter and spring and four experimental seston treatments. *M. edulis* growth data corresponding to spawning in autumn are indicated by filled circles.

In order to relate growth to food concentration, future studies will probably benefit from a better characterization of the nutritional value of the seston (Pouvreau et al. 2006; Ren *In press;* Rosland et al. *In press*), in conjunction with the bivalve's ability to utilize (i.e. absorb) the seston. The characterization of seston according to its carbohydrate, protein and lipid content (e.g. biopolymeric content) seems promising (Danovaro and Fabiano 1997). However, obtaining the biopolymeric content of the seston might not be sufficient to explain growth, because feeding responses to certain phytoplankton species can influence feeding rate, physiology and cause mortality (see Section 1.2). Additional factors may come into play as bivalves have chemosensory abilities and the feeding rate may be inhibited (Ward and Targett 1989) or stimulated (Ward et al. 1992; Navarro et al. 2000) by phytoplankton metabolites.

The interpretation of *M. edulis* growth responses suffers from the deficiency of significant increases in dry flesh weight at ambient and slightly dilute seston concentrations (treatment 1 and 2) during autumn, and asymptotic growth in mussels could not be evaluated. The lack of positive dry flesh weight growth during autumn was likely caused by minor spawning events (Duinker et al. 2008). Excluding autumn growth data in treatment 1 and 2 from Figure 4, the positive dry flesh weight growth detected appears linear at all measures of seston quantity.

Marine bivalves exhibits seasonal cycles of energy storage which are utilized in conjunction with available food to meet their energetic requirements (Macdonald and Thompson 1986; Strohmeier et al. 2000). Variations in the mass of tissue compartments indicate either accumulation or storage of substrates (Barber and Blake 1981). The seasonal changes in *P. maximus* dry flesh weight was linearly related to the changes in the striated adductor muscle putting forward this organ as the most important energy storage and energy allocation site under these low seston conditions (Paper II). This holds up even if the energy content of uneven biochemical composition of organs is considered (*P. maximus* digestive gland and gonad contains more lipid, (Strohmeier et al. 2000)) because the changes in striated adductor muscle mass was about 6 times larger than the combined changes in gonad and digestive gland mass. Although of less importance in an overall energy budget, clear seasonal mass changes across seston treatments was recorded in other tissue compartments. These mass changes, in addition to the available food, suggest that gonad and digestive gland (treatments 2-4) have contributed to meet the metabolic cost during autumn (Strand and Nylund 1991a; Duinker and Nylund 2002), while during winter the striated adductor muscle and remaining tissue (mostly treatments 3 and 4) appeared to meet the metabolic needs.

Post-winter starvation, *P. maximus* given diluted seston quantities (treatment 3) allocated energy to the digestive gland before the gonad (Paper II). It may be speculated that the initiation of gametogenesis commences only after a sufficient accumulation of energy reserves in the digestive gland. Strohmeier et al. (2000) also reported rapid growth in the digestive gland of *P. maximus* following winter starvation. This growth was mainly caused by an increase in the protein content. Proteins may represent enzymes functioning in the digestive activity of the digestive gland (Lepennec et al. 1991), and the rapid growth in the digestive gland may have been to increase the digestive capacity at the high food concentrations occurring at low temperatures during the spring bloom.

3.3 Feeding physiology and net energy balance

The physiological response of bivalves to environmental change have been widely studied (reviewed by Bayne and Newell 1983; Hawkins and Bayne 1992; Bayne 1998), generally reporting that bivalve filter feeders regulate food capture and utilization according to nutritional needs (Hawkins and Bayne 1984; Bayne et al. 1988; Bayne et al. 1993; Bayne 1998). Several pre- and post-ingestive mechanisms have been identified by which bivalve filter feeders actively compensate for a variable food supply. These include the regulation of feeding rate, the selective retention and rejection of particles, selective absorption and variable absorption efficiency (Section 1.3).

3.3.1 Energy acquisition

In the absence of any regulation of feeding and digestion processes, temporal variation in ingestion and absorption rates would be dependent on changes in the food supply and other constraints on feeding (e.g. temperature, salinity, contaminants, etc). Numerous empirical studies have shown that seston concentration has a strong influence on bivalve clearance rate and explains a large fraction of the variance in clearance rate measurements (Navarro and Winter 1982; Iglesias et al. 1996; Hawkins et al. 1998b; Hawkins et al. 2001; Velasco and Navarro 2002; Velasco and Navarro 2005; MacDonald and Ward 2009). The bivalves prominent feeding adaptations to low food concentrations reported in Paper I increased the energy acquisition of a relatively high quality diet, and contributed in the positive tissue growth under conditions that previously would have been expected to result in a negative net energy balance. The major determinant role of clearance rate to modulate energy acquisition is in accordance to previous studies on suspension feeding bivalve molluscs feeding at higher

food quantities (Hawkins et al. 1999; Gardner and Thompson 2001; Hawkins et al. 2001; Cranford et al. 2005).

Ingestion rate increases with higher seston concentration (Winter 1978; Bayne et al. 1989) and maximum ingestion is limited by the filling capacity of the gut (Widdows et al. 1979). Saturation of the digestive system has been reported to occur in *M. edulis* (1 g dry tissue weight) at 6.5 mg POM h^{-1} (Hawkins et al. 1997), a rate which is more than twice the highest mean value obtained in Paper II (2.9 mg POM h^{-1}). This value was 4.4 mg POM h^{-1} for *P. maximus* but no "digestive saturation value" is available for this species in the literature. There were no indications of saturation of the digestive system as the bivalves did not produce pseudofaeces and the ingestion rate was directly related to the POC concentration in the treatments since the clearance rate was most often stable. This finding comes with one important deviation recorded for *P. maximum* given shallow water and caused by a reduction in clearance rate during the spring blooms (Paper I). This clearance rate decrease in spring resulted in a 1.6 times lower ingestion rate compared to *M. edulis,* and partly explain the lower growth rate obtained for *P. maximus* during spring (Paper II).

Food quality can be a major constraint on the bivalve energy budget. The size distribution of particles, the balance in the diet between biologically inert and metabolizable fractions and the biochemical composition of this metabolizable fraction are important to understand the bivalve feeding behaviour (Bayne et al. 1987). Absorption efficiency is the best indicator of diet quality (Charles et al. 1995) and is predictable on the basis of diet quality i.e. it decreases exponentially with a progressive increase in dietary inorganic content (Navarro et al. 1991; Navarro et al. 1992; Cranford 1995; Hawkins et al. 1996; Iglesias et al. 1996; Urrutia et al. 1996; Barille et al. 1997; Hawkins et al. 1998a; Hawkins et al. 1999; Velasco and Navarro 2005). In Paper II the bivalves showed no apparent adaptations of absorption efficiency to the narrow span of seston quantity and quality provided. The absorption efficiency of both species was generally in the upper range for mussels feeding on natural seston (Bayne et al. 1987; Bayne and Hawkins 1990). This is in agreement with the assumption that high absorption efficiency is expected at high diet quality (Cranford 1995; Grant et al. 1997; MacDonald et al. 1998). The energy acquisition is very sensitive to absorption efficiency and the high values recorded in Paper II have contributed to the low net zero energy balance found for these bivalves residing in a low seston environment. As there were no seasonal patterns in

absorption efficiency the absorption rate showed the same close relation to POC as ingestion rate.

3.3.2 Energy expenditure

The bivalve's regular activity to the seston treatments is in the following text referred to as routine respiration. The routine respiration in both species was linked to the seasonal variation in POC quantity when provided ambient seston concentrations (Paper II). It decreased during autumn, was low during winter and increased and decreased in conjunction with the two phytoplankton blooms. The pattern of routine respiration showed similarity to the temperature development but deviated from the temperature progress during the spring phytoplankton blooms. Vahl (1978) also found that the seasonal changes in oxygen uptake of *Chlamys islandica* was explained by the food availability, whereas the temperature did not affect the seasonal pattern. The relationship between routine respiration and seston quantity became less clear in the diluted seston treatments, and this represents the detected adaptations of respiration rate to the treatments provided, i.e. the bivalves reduces the energetic cost when food quantity declined. Metabolic rates have previously been reported to be highly responsive to food levels (Grant and Thorpe 1991; Pilditch and Grant 1999a) and reproductive state (Bayne and Widdows 1978; Vahl 1978; Smaal et al. 1997). Although gonad rebuilding in *P. maximus* was detected during spring, the respiration rate decreased with lower seston quantities in-between the two phytoplankton blooms. A lack of a correlation between oxygen uptake and gametogenic activity has been reported by MacDonald and Thompson (1986) in *Placopecten magellanicus*. In sum this points to the routine respiration being forced by changes in food quantity, likely caused by the energy demand of digestion as food acquisition may require little energy (Bayne and Hawkins 1990; Willows 1992).

The seasonal respiration rate for *P. maximus* across treatments typically showed similar values and overlapping confidence limits. However, the respiration rate in *M. edulis* given the highest seston treatment was unexplainably lower compared to the three other treatments. The mean ratio of metabolic to absorbed energy at ambient food concentrations during autumn and spring (neglecting *P. maximus* during spring due to strongly depressed clearance rate) was 0.2 to 0.3, indicating that the bivalves acquired 3-5 times more energy than they metabolized. The decrease in energy content in tissue mass during winter was similar to the metabolic cost for *P. maximus*, while the metabolic cost of *M. edulis* during winter was higher compared to the lost tissue mass. This indicates that *P. maximus* did not absorb the ingested particulates during

winter contrary to *M. edulis*, which adds as an explanation to the observed differences in dry flesh weight growth capacities in these two species during winter.

The ammonia excretion rates reported in Paper II constituted a minor fraction of the energy expenditure. The molar ratio of oxygen consumed to nitrogen excreted (O:N) indicates the proportion of protein catabolised relative to the carbohydrates and lipids (Conover and Corner 1968). This ratio points to protein catabolism during the low food quantities in winter for both species in all seston treatments. This is consistent with the co-occurring decrease in dry flesh weight and degradation of the striated adductor muscle (Strohmeier et al. 2000). The O:N ratio declined in the deep water treatment during the experiment, indicating an increase in protein catabolism as time passed. The patterns in the O:N ratio were consistent with dry flesh weight changes observed during the experiment.

3.3.3 Net energy balance

Bayne et al. (1987) studied feeding and digestion of *M. edulis* in mixtures of silt and algal cells at low concentrations (0.07-0.32 mg POM L^{-1}, 7-55 POM%) and reported that the net energy balance increased with elevated organic content of the seston as a result of both a higher ingestion rate and increased absorption efficiency. However, relationships between seasonal variations in feeding activity and seston abundance or nutritional quality have proven to be difficult to establish (Cranford and Hill 1999) owing partly to the large simultaneous changes in seston quantity and quality, and to the constraints on characterizing food value (Pouvreau et al. 2006; Ren *In press;* Rosland et al. *In press*). In low seston environments comprising high food quality, where the underlying eco-physiological compensation appear less complex, the net energy balance seems most driven by high clearance rate and absorption efficiency (Paper I and II). This was supported by the close relation between net energy balance and POC quantity. This finding comes with one exception detected for *P. maximus* given ambient seston concentrations during the phytoplankton blooms, when a marked decline in clearance rate strongly decreased the net energy balance.

Although few physiological responses were detected to the low food quantities provided, the estimated NEB did not accurately predict the observed growth and in particular overestimated growth during autumn and winter. Any release of gametes, as plausibly occurred in *M. edulis* during autumn, would lead to an overestimation of NEB. However, the discrepancy between estimated and observed growth seems mostly related to the properties of the seston.

NEB is an instantaneous measure of a continuous process and the accuracy of NEB estimates rely on the frequency of the eco-physiological measurements according to the environmental forcing. As there are large changes in seston concentration and nutritional value on both a short and long-term scale (Section 1.2) the frequency of measurements may have been insufficient to reflect the seasonal feeding behavior and physiological responses to short-term changes in the seston. This study points to scallop clearance rate as most sensitive to changes in seston quantity while the other eco-physiological traits seem to be modestly regulated according to seston quantity, quality and temperature provided. However, it is important to catch any short time variation in seston characteristics as variation in the energy content of the seston directly influences the energy budget.

Most net energy balance studies are based on a fixed energy content assigned to the seston mass ingested, and typical energy contents are 20.78 J mg^{-1} POM (Crisp 1971) and 47.7 J mg^{-1} phytoplankton POC (Platt and Irwin 1973). However Danovaro and Fabiano (1997) showed that there are seasonal variation in the ratio of the sum of carbohydrates, protein and lipid of organic matter (biopolymeric fraction, BPF) to POC. They reported the mean annual contribution of BPF-carbon to 58% of the total organic pool (POC) while protein accounted for 48% of the total nitrogen pool. The remaining fraction of the organic carbon and nitrogen was composed of material of more refractory composition of geopolymeric origin, possibly bound into macromolecular refractory compound and likely not readily available to benthic consumers. In net energy balance studies the net absorption efficiency is measured and represents the actual fraction of seston assimilated, but the net absorption efficiency does not account for any variations in the energy content of a fixed seston mass. The mean energy content of POC during spring, summer and autumn-winter can be calculated from Danovaro and Fabiano (1997) to 33.2, 28.4 and 27.2 J mg^{-1} POC respectively. The variation between seasons represented 18%, but it should be emphasized that these are based on mean values and do not reflect any short-time variation occurring within the season. The mean energy content of POC obtained by Danovaro and Fabiano (1997) are from 30 to 43% lower compared to Platt and Irwin (1973). This suggests that the energy content of the seston should not be treated as a constant, and our net energy balance estimates would increase in precision, both between seasons and in scale to observed growth by using the above mentioned values. Future NEB studies will most likely benefit from using a variable energy content of ingested

matter based on the BPF content of the seston and possibly also by determine the net absorption efficiency on the basis of BPF in the food and faeces.

The aquaculture potential of bivalve mollusks is directly related to their zero NEB, detected at 80 µg POC L^{-1} and 0.4 µg Chl *a* L^{-1} in Paper II. The low zero NEB and the positive growth obtained indicate an aquaculture potential, although the species production capacity to low seston environments remains to be evaluate. The ability to exploit and grow under the low food concentrations was primarily caused by continuous feeding at high rates and a high efficiency in absorbing the available food. This feeding strategy seems necessary for suspension-feeding bivalves residing in the environmental extreme of low food concentrations. The net energy balance predictions of growth did not fit the observed growth, plausibly due to an inadequate characterization of the nutritional value of the seston. The information obtained in Paper I and II is determinative to interpret biogeographical distribution, nutrient cycling and risk of food depletion in bivalve habitats or culture operation.

3.4 Seston depletion

The environmental concern of bivalve farming is typically related by their trophic level effect (top-down and bottom-up controls) on the ecosystem (Cranford et al. 2008; Grant et al. 2008). The concept of seston depletion originated with studies in bays and estuaries where suspension feeding bivalves constituted the major grazers. The volume of water filtered was compared to the sea water exchange (Officer et al. 1982; Dame 1996; Wildish and Kristmanson 1997) and in 10 out of 13 systems, residence time was longer than clearance time indicating that the bivalves regulate their food source (Dame 1996). The large capacity of bivalves to clear water of seston can also result in depletion in suspension culture (Navarro et al. 1991; Heasman et al. 1998; Ogilvie et al. 2000; Grant et al. 2007; Cranford et al. 2008; Grant et al. 2008; Petersen et al. 2008; Strohmeier et al. 2008); Paper III). The degree of depletion mainly depends on the rate at which the seston is replaced by lateral advection (Roegner 1998) and phytoplankton growth, but it has also been related to ambient seston quantity and quality, bivalve physiology, stocking density and cultivation unit layout/design. When seston consumption rate exceeds the replacement rate, the bivalves may become food limited and the production carrying capacity is exceeded for that site (Cranford et al. 2008). If bivalve suspension feeding induces seston depletion over a significant proportion of the

ecosystem it may affect the base of the marine food web and raise ecological concerns to other components of the ecosystem. The high bivalve feeding rates detected at low seston concentrations (Paper I) increases the risk of seston depletion compared to lower the feeding rates reported at higher seston quantities (Section 3.1). This demonstrates the importance of possessing knowledge on appropriate stocking density to provide sufficient food resources to bivalves according to the environments carrying capacity.

The replacement of seston within a cultivation unit is primarily forced by lateral advection since the residence time of sea water is typically too short for significant phytoplankton growth. The frequency of advected food may be regular, as when forced by tidal currents or irregular, as when forced by wind or fresh water runoff. The local current regime thereby determines the regularity of new food supply, and seston depletion is more likely to occur during periods of low flow. The current direction was observed to align with the direction of the long-lines due to friction-induced channelling of water flow through the unit length (Strohmeier et al. 2008; Paper III). The current speed has been reported to decrease inside rafts (Boyd and Heasman 1998; Petersen et al. 2008) and inside long-line units (Strohmeier et al. 2008; Paper III). The flow reduction is likely caused by the friction imposed by the bivalves (Wright et al. 1997; van Duren et al. 2006); Paper III) in conjunction with the layout of the cultivation structure (Boyd and Heasman 1998); Paper IV). In units containing several long-lines that are closely spaced, the flow tends to diverge around and underneath the cultivation unit (Boyd and Heasman 1998). Paper IV contains a model that can aid in optimizing flow through bivalve cultivation units according to the units layout (see below).

Bivalve cultivation in ecosystems containing high food concentrations will naturally be less prone to seston limitation compared to environments showing low food concentrations. In farming units, the food concentration typically decreases from the entrance to the exit (Navarro et al. 1991; Petersen et al. 2008; Strohmeier et al. 2008); Paper III). Depletions of Chl *a* in the range from 20 to 60% have been reported in low seston environments (Cranford et al. 2008; Strohmeier et al. 2008); Paper III). The depletion plume leaving the unit downstream may extend several times the length of the unit (Fig. 5) (Cranford et al. 2008) making this area less suitable for bivalve farming (Grant et al. 1993). The capability of bivalves to select among food particles (Section 1.3) may reduce the food quality downstream and the combined changes in food quantity and quality can influence on the feeding physiology of bivalves. This was shown by Navarro et al. (1991) that compared the

physiological energetic of mussels situated in front and behind of rafts. They reported consistently higher scope for growth for mussels in front of the raft. This result was not only due to improved feeding condition in the front of the raft, but the mussels also showed higher clearance rate and absorption efficiency. The higher scope for growth in the front of the raft was confirmed by empirical evidence on growth rates. This is consistent with the decrease in current speed, Chl *a* concentration and mussel condition index detected from the edges and toward the center, reported for the long-line farm in Paper III.

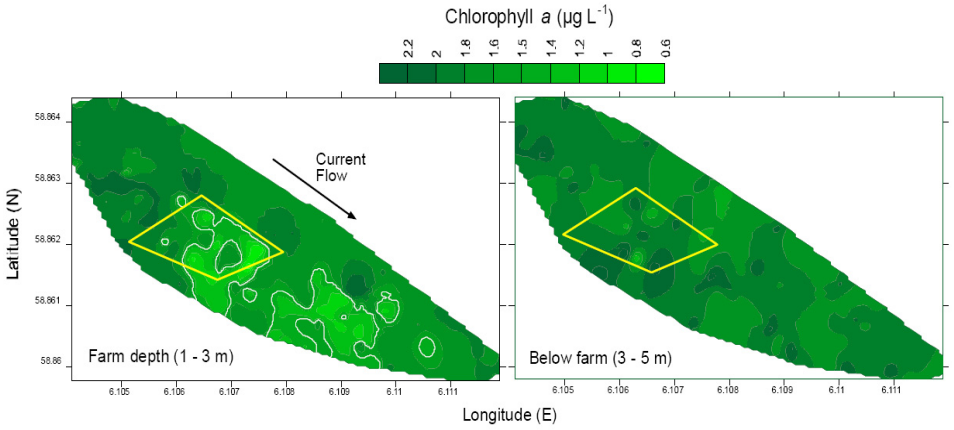

Figure 5. Example maps of the phytoplankton biomass (chlorophyll *a*) around a mussel farm (outlined in yellow) in Høgsfjord, Norway showing food depletion within the depth zone of the farm (left), but not up-current (left) or below the farm (right). Contours outlined by the white line represent the zone exhibiting greater than 20% food depletion. Figure from Cranford et al. 2008.

Heasman et al. (1998) showed that seston depletion intensifies with increasing bivalve stocking density and age (size), both as food extraction increases and water exchange decreases at higher mussel density/biomass. Subsequently, a higher yield of marketable mussels was obtained from rafts with a low stocking density compared to higher stocking density. Clearly, the cultivation of bivalves at high densities and at low food concentrations increases the risk of food limitation, and farming in low seston environments will benefit from management tools that can provide guidelines to maintain sufficient availability of food through cultivation units.

The consequences of seston depletion will in part be determined by the the magnitude and persistence but also the scale at which seston depletion occurs. Seston depletion primarily influences growth, but in extreme cases of food limitation it may lead to mortality (Grant et

al. 1993). Decreased growth rates naturally increase grow-out and production time, which increases bio fouling, handling and harvest time. Seston depletion can lead to spatial variations in growth or meat yield (Paper III, Strohmeier et al. 2008) and variable consumer quality. All of these factors will negatively impact on the economic viability of bivalve farming.

In order to reduce the risk of seston depletion in bivalve culture, we can seek to modulate the factors controlling seston depletion. To improve the seston supply to cultivation units located in low currents there is the obvious option to move the unit to an area with a higher background current speed. To ensure a regular supply of new seston the unit will benefit from being located in a current regime driven by the tides. To minimize the loss of the background current speed through a culture unit Paper IV present a model that estimates the current speed reduction according to culture unit layout. This model can be used to predict optimal cultivation design according to the ambient current speed. The model predicts average current speed within the unit to increase progressively as the length of the unit decreases and this trend is strongest at high background current speeds and for short units (i.e. 50-100 m). The volume of water moving through the unit (transport of food) is in addition to the ambient current speed dependent on the entrance area of the farm. Therefore, if we consider a cultivation unit with a fixed surface area, then the transport of seston through the unit increases much more rapidly than the current speed alone when the length of the unit is reduced (e.g. entrance area becomes larger). The current speed inside a farm is progressively reduced when the spacing between long-lines (S) decreases (Fig. 6). The effect of increasing spacing between long-lines on the current speed inside the farm is largest for short units that have narrow spaced long-lines.

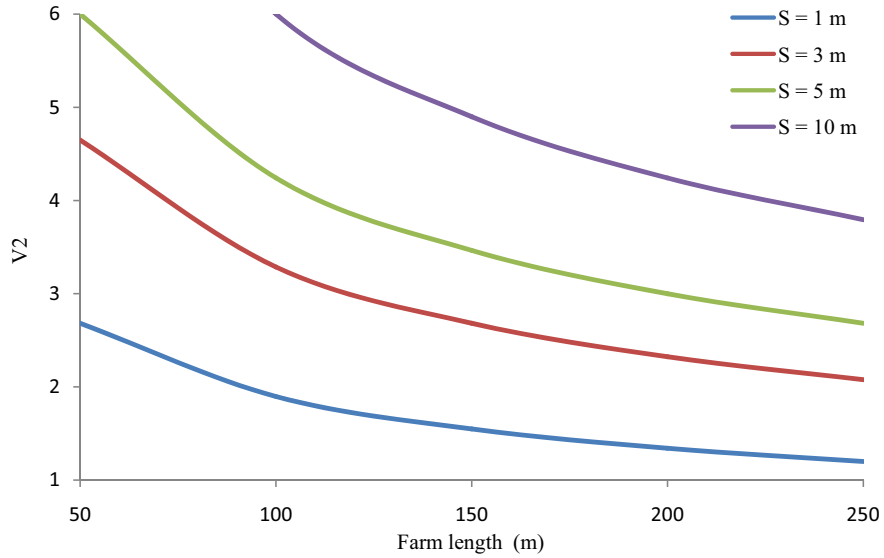

Figure 6. The current speed within a farm (V_2) calculated as a function of farm length at four spacings between long-lines. The background current speed (V_1) is 6 cm s^{-1}. The measured current speed is averaged from 5-7 cm s^{-1}. Figure is from Paper IV.

To increase the seston supply within units we can reduce the length of the unit, increase the spacing between long-lines and mussel ropes, move the unit to an area of higher background current speed, or provide a combination of these alternatives. There is a strong increase in the current speed inside short units (~ 50 m) when moved to a greater background current speed, but units longer than 100 m should be reduced in length rather than moved to a greater background current speed. Enlarging the space between the long-lines will increase the current speed inside the cultivation unit at all lengths. Grant and Bacher (2001) developed a numerical model for flow modification induced by suspended aquaculture and their results indicated that disregarding the physical barriers associated with culture will result in a serious overestimation of particle renewal and thus an overestimation of carrying capacity.

Paper IV also presents a box model of production carrying capacity of mussels. Considering the full range of possible cultivation unit designs (using a fixed total surface area) from a width-length ratio (W/L) of 0.1 to a square farm (W/L = 1), the modelled production capacity increases substantially as the width-length ratio (W/L) rises for current speeds from 4 to 8 cm s^{-1} (Fig. 7) and as the Chl *a* concentration increases (Paper IV). The effect of increased background current speed on the carrying capacity was prominent at W/L > 0.5, but is

practically unimportant at low W/L, around 0.1- 0.2. This suggests that redesigning long-line mussel units can greatly enhance their production carrying capacity.

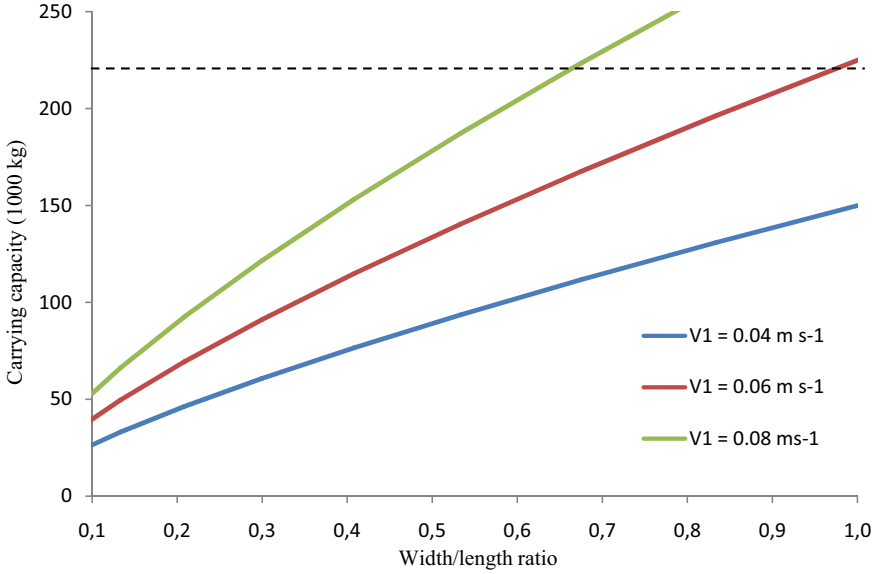

Figure 7. Farm production carrying capacity at three background current speeds, as a function of width/length ratio (W/L). A W/L = 1 is a square farm and a low W/L (0.1) is a long and narrow farm. Surface area is fixed at 3000 m^2, H is 5.5 m, S is fixed at 1.5 m, C_1 is 1.8 µg Chl *a* L^{-1} and C_t is 0.7 µg Chl *a* L^{-1}. Broken horizontal line indicates a biomass of 220 tonnes or 10 kg mussels m^{-1} rope. Figure is from paper IV.

There is variation in the seston quantity along the Norwegian coastline and differences in food concentrations among fjords are probably related to the influx of nutrients from deeper water strata to the euphotic zone (Aure, J., personal communication). To increase ambient seston quantity we can stimulate phytoplankton production by forced upwelling of nutrient rich deep water. This method has increased summer phytoplankton biomass by three times during two consecutive years in an area of 10 km^2 in a Norwegian fjord (Aure et al. 2007). However, high phytoplankton concentration may have a stronger effect on *M. edulis* growth rate compared to *P. maximus,* caused by the reduction in *P. maximus* feeding rate detected at high phytoplankton concentration (Paper I). Disregarding the feeding responses, both bivalve species will likely benefit from the improved nutritional value of phytoplankton, and high ambient seston concentration should increase the production capacity within the upwelling area.

4. CONCLUDING REMARKS AND PERSPECTIVES FOR THE FUTURE

This study has shown that *P. maximus* and *M. edulis* residing in a low seston environment do not stop suspension-feeding, but maintain high feeding rates at even the lowest seston quantities. The bivalves showed a net zero energy balance at seston concentrations of about 80 µg POC L^{-1} and 0.4 µg Chl *a* L^{-1}, which is less than half the values previously reported for bivalves. The study shows that these species grow in low seston environments which indicate that far more habitats can be used to farm bivalves. The low net zero energy balance detected was primarily caused by the high feeding rates and high net absorption efficiency. The data in Paper I and II have been used to improve parameter estimations for a mussel growth model based on dynamic energy budget (DEB) theory, applicable to low seston environments (Rosland et al. *In press*). This model have been coupled to the farm (population) model presented in paper IV, and provide mussels growth as a function of stocking density and farm design (Rosland et al. 2009) and may be used in the management, production estimates and site selection of bivalve aquaculture in low seston environments.

Results from Paper III and IV have been used in management advice to the Norwegian mussel farming industry mainly by contributing in the redesign cultivation units (i.e. extending the spacing between long-lines and shorten the length of long-lines). Paper III and IV have also increased the awareness of measuring the environmental forcing as current speed and food concentration before choosing a farm site and applying for a farming license. This study has provided a better understanding of interactions between the environment and bivalve farming, and the results have also contributed to the development of an operational web based tool (GIS based) for locating sites for mussel culture (Hageberg et al. 2009). In summary, this work has contributed to the knowledge on bivalve feeding physiology at low food concentrations in general, and in aquaculture specifically, aiding in improving the bivalve production capacity and site selection in a low seston environment.

Among the topics which require more research is the proximate cause of the high clearance rates obtained in the low seston environment. Future work should reveal if the high clearance rates are linked to the gill:labial palp ratio or are the net result of low seston quantity and high seston quality. The cause of the decrease in scallop feeding rate during the phytoplankton blooms also remains unclear, but may be linked to harmful phytoplankton species. The study

emphasize that more knowledge is needed on the relationship between the nutritional value of the seston, bivalve tissue growth and feeding physiology.

Despite frequent seasonal sampling of the physiological components of growth, net energy balance predictions for both species overestimated actual growth. The main factor suspected to cause this mismatch is the inability of bulk seston characteristics to adequately characterize the seasonably variable energy content of the seston. Future studies should avoid utilizing a fixed energy content of ingested seston, and to increase the accuracy of growth estimates it is suggested to include the seasonal variation in the biopolymeric constitute of seston. Mussel growth estimated by the DEB model at low seston concentrations matched the observed growth fairly well (Rosland et al. *In press*) and it appears as a robust alternative to growth estimates based on the net energy balance of bivalves.

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